

# EFFECTS OF THE PLEISTOCENE ON NORTH AMERICAN INSECTS<sup>1</sup>

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## INTRODUCTION

The state of our knowledge of the effects of the Pleistocene on the present patterns of insect distribution is, at best, inadequate. Many of our conclusions must be based, in part, on geological and botanical evidence, and this literature, pertinent at least in some degree to any analysis of Pleistocene effects on the biota, is vast. Many papers dealing with taxonomy, evolution, or biogeography often contain sections pertinent to the present topic and the reader should refer to the review by Munroe (1965), Ross (1965), and Frey (1965) to supplement the information and literature discussed herein. This paper is not entirely a review, but includes some original interpretations and a discussion of problems.

A number of difficulties are inherent in any consideration of the historical aspects of insect zoogeography as it relates to the Pleistocene. Before the effects of the Pleistocene can be considered in any meaningful way, several assumptions concerning the origin and evolution of the North American insect fauna must be made. To do this is difficult, for not only are adequate fossil records lacking in most insect groups (Martynova 1961; Pierce 1957), but we are dealing with a tremendously diversified fauna having various origins (Ross 1953; Mayr 1963a), methods of dispersal, and rates of evolution and speciation. The understanding and application of at least some of the following assumptions are helpful in any attempt to correlate today's insect distributions with past events.

The first assumption is, at least for the more advanced orders, that the Old World has been the center of origin for many of the ancestors of our North American insects. In general, I have found no entomological evidence that refutes the excellent works by Darlington (1957, 1965) on the dispersal routes of the vertebrates, and his analysis of the origins of the southern cold temperate fauna. This assumption does not mean that genera and even tribes or families of insects have not developed entirely within the confines of the New World (Ross 1953). It merely states that the general dispersal pattern has been from the Old to the New World, with the Beringian area being the most important invasion route.

My second assumption is that the more primitive orders, Orthoptera (particularly the roaches), Neuroptera, etc., on the average, have shown a

<sup>1</sup> The survey of the literature pertaining to this review was concluded in January 1968.

distinctly slower rate of evolution at the generic level and above than have some of the more advanced orders, such as the Hymenoptera, Diptera, and Coleoptera. However, on the species level, evolution and speciation may have been rapid or slow in any order. Some aspects of these evolutionary problems are discussed by Briggs (1966).

The question of evolutionary rates (with speciation as a type of evolution, Mayr 1963b) remains one of the most difficult obstacles to any meaningful analysis of the effect of past events on the present insect fauna (Ross 1965). Mayr (1963b) has presented a masterly summary of the general subject, but lack of an adequate fossil record leaves the historical aspects of the evolution of many major groups of insects largely in the realm of speculation. However, in order to interpret any of the evidence on speciation as we now see it, some evolutionary assumptions must be made. Seemingly, insects can evolve rapidly or slowly. The rate of evolution and the average time required for the formation of species almost certainly varies with conditions, a rapidly changing environment having a different effect on speciation and extinction than a stable one.

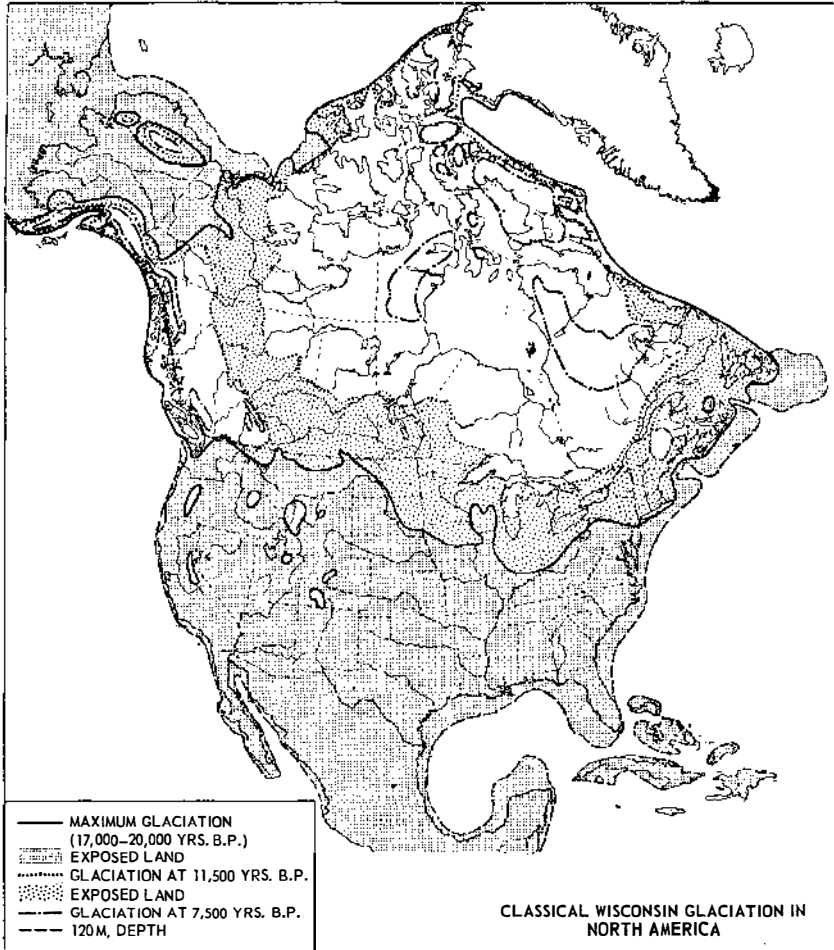
Based on this reasoning, the third assumption is that there is a strong correlation between the rate of speciation (and to some degree the rate of evolution) of insects and the changes that occur in their hosts or niches. If this is true for even 50 per cent of our extant species, it gives at least a partial basis for speculation. Mention of a few illustrations seems warranted. Buprestidae of the genus *Trachykete* that bore in cypress and related primitive trees, seem to be more primitive than genera of Buprestidae that bore in willows, oaks, etc. Many of our plant-feeding sibling species of chrysomelid beetles (Brown 1959) that seem to have recently speciated are associated with plants which seem to be currently diversifying, such as *Salix* and *Crataegus*. Leppik (1963, 1966) hypothesized that there was a sudden rapid evolution and speciation in flower- and pollen-feeding insects at the time when flowering plants were rapidly diversifying. In the scarabaeid genus *Onthophagus* there are closely related species (Howden & Cartwright, 1963) occurring with different species of *Neotoma* (wood rats). I doubt if these complexes of beetles evolved before either plants or wood rats speciated, the same factors, in each case, seemingly effecting both. However, it is important to stress that many other factors can effect speciation, such as geographic isolation of similar habitats, etc., and that the above assumption applies to only certain cases and then perhaps only to a certain percentage.

The last assumption is that the longer a major geographic area has remained moderately stable climatically, the more diversified its flora and fauna (Downes 1964). In some ways this seems to argue against the third assumption, but in a stable habitat more niches develop (diversified soil formation, variations in relief by erosion, etc.), and there is more time for invasion and specialization within these niches. This is essentially a slow process and is intimately related to the size of the area having a stable climate (Darlington 1959; Wilson & Taylor 1967).

In addition to these assumptions, several other factors should be emphasized. A thorough knowledge of the taxonomy, habits, and dispersal powers of a group is needed before any detailed analysis of its past history can be meaningful. Also, before we can reach any conclusions concerning the effects of the Pleistocene, it is necessary to attempt to deduce what type of conditions prevailed before that period. This must be considered in order to speculate on the type of biota being affected by the changes occurring during the Pleistocene. Here again we are badly handicapped by the lack of fossils from both before and during the Pleistocene. Because of this, even though we know that there were a number of glacial periods during the last 1,500,000 years, it is extremely difficult, if not impossible, to attempt to correlate present insect distribution with any particular glacial advance, with the possible exception of the last ice maximum during the Wisconsin. This is often referred to as the "Classical Wisconsin Glaciation" (see map).

#### PRE-PLEISTOCENE ENVIRONMENTS

While some climatic fluctuations (Dorf 1960) occurred during the early Tertiary, North America at that time was largely covered by tropical and subtropical forests. General climatic deterioration became pronounced during the Miocene, the cooling producing a noticeable botanical effect (Barghoorn 1963; Dorf 1960). Also in the early and middle Tertiary, tectonic uplifting, particularly in western North America (King 1958; Mengel 1964), produced a rain shadow effect which led to the formation of the prairie regions. By the end of the Miocene the southwestern desert formations were well established (Axelrod 1958; Cohn 1965), with most of the present-day plant genera represented. Considering the botanical evidence, and the meager fossil insect evidence from the Oligocene Florissant shales (Pierce 1957) it seems likely that most of our extant genera of insects were also represented at this time. The cooling trend continued throughout the Pliocene (Dorf 1960; Barghoorn 1963; Hays & Opdyke 1967), with tundra, coniferous forest, and large areas of temperate forest becoming widespread in the northern half of North America. However, it seems unlikely that these formations were truly a counterpart of these northern formations as we now know them (Braun 1950, 1955), since it was only through the leveling and grinding action of the glaciers that the large northern areas of low relief, poor drainage, and immature soils were formed. The time necessary for the development of the insect faunas associated with the major floral elements varied, the tropical and subtropical elements dating from the pre-Tertiary, the temperate deciduous elements developing largely during the Tertiary, the arid-adapted and prairie fauna originating during the early Miocene, and the northern faunal elements arising largely during the Pliocene. If this rough approximation of events is true, then it seems rather unlikely that there was ever, during the Tertiary, a large assemblage of truly cold-adapted insect species existing in northern North America. Many of our cold-adapted insect species could have evolved in montane regions as postulated by Ross (1953) for some Trichoptera, then moved northward follow-



Classical Wisconsin Glaciation in North America. Glacial boundaries for the different times are based on maps compiled by Dr. V. K. Prest, Geological Survey of Canada. (B.P. = before the present.)

ing the glaciers, rather than evolving in northern areas and migrating southward. Ross (1958) states that "The relatively flat portions of the present day northern tundra and coniferous forests are sufficiently extensive to have an air of permanence. If, however, they were stable features of the landscape, geologically speaking, one would expect some distinctive taxonomic units to have evolved and remained therein. Among the insect groups of my acquaintance, the species of the flat north country are either the same as those in the western or eastern mountains or were obviously derived relatively recently from montane species." Almost certainly, cold-

adapted species of insects evolved in both northern (Beringian) and montane habitats, but the present evidence is still too meager to make any meaningful assumptions on the early origins of all of the cold-adapted fauna.

#### PLEISTOCENE CLIMATES

The factors that led to the climatic deterioration culminating in the series of Pleistocene glaciers are still largely unknown. Mitchell (1965) has discussed the various theories and presented an excellent summary of the possible reasons for the climatic changes. From evidence presented by Mitchell and also by Lamb (1965), and Broecker et al. (1968), it seems unlikely that any one factor was responsible, but that an interaction of factors, such as the earth's orbital variation and auto-variation of air and ocean currents, was responsible. Whatever the reasons, there was a series of glacial advances and retreats which has lasted at least 1½ million years. North America was supposedly subjected to four great "ice ages," the Nebraskan, Kansan, Illinoian, and Wisconsin. However, recent evidence indicates that there were more than four major glacial advances in North America. The exact number remains in doubt.

The precise number of glacial advances and retreats, while important, does not affect the general impact that they have had on the North American fauna. The effect differs in many ways from similar fluctuations in Europe (Zeuner 1959; Müller-Beck 1966). In Eurasia the major mountain ranges run approximately east-west while in North America they are largely north-south oriented. The different topography has resulted in the climatic changes having a very different effect on the two biotas. In North America the main questions are, how much north-south movement was there, how much east-west fragmentation of habitats was there, how far south did the climatic changes (not just glaciation) show a discernible influence on the insect fauna, and what was the total effect of the Pleistocene on the composition of the North American insect fauna as we now know it?

It seems best to attempt to answer these questions by starting with a general discussion of events in North America and ending with a more detailed regional analysis.

#### GENERAL EFFECTS

The question as to how far to the south the influence of the Pleistocene climatic changes had noticeable effects is nearly impossible to answer adequately. A general world-wide depression of temperature seemingly occurred with mountain snow lines being depressed during pluvial periods at least as far south as Mexico City (Flint 1957). However, there is a considerable body of evidence that indicates that even if temperature depression was fairly uniform, which seems rather unlikely (Dillon 1956), the effect on the biota was not uniform because of different habitat requirements, dispersal powers, etc. Seemingly, the tropical areas of the world remained relatively unchanged, the time-stability factors being more optimal there than in more temperate regions. If this is true, then the percentage of endemism

(considering only large continental land masses) should be highest in those areas least affected by the climatic changes. This reasoning is based on the supposition that forms endemic (restricted and native) to the various major "zones" of the Americas, i.e., eastern deciduous forests, deserts, etc., often have (at least at present) relatively restricted ranges and hence would be eliminated more quickly than more widely ranging species which, by implication, are eurytopic. The following compilation of the New World genera of the beetle family Scarabaeidae seems to support this reasoning.

TABLE I  
NEW WORLD GENERA OF SCARABAEIDAE\*

	Canada	U. S.	Mexico (N. of Isthmus of Tehuantepec)	Central America	Brazil	S. America exclusive of Argentina and Chile	Argentina
Total no. of genera	35	111	133	144	179	250	118
No. of endemic genera	0	13	20	33	41	72	29
% endemics	0%	11.7%	15%	23%	23%	28.8%	24.5%

\* The above figures were compiled from catalogues and do not include either recently described genera or imports. Political boundaries are normally not useful in a zoogeographic sense; however, in the above table, the southern boundary of Canada roughly approximates the southern edge of the last glacial maximum, the United States and Mexican faunas have been and are separated by a desert barrier (Howden 1963), and the Mexican genera cited are those found north of the Isthmus of Tehuantepec. In the other cases the format of the catalogues necessitated the use of political divisions.

We know that the Pleistocene glaciations covered most of Canada, producing during each major glaciation almost a complete biological vacuum. Using the percentage of endemics and allowing some variation for differences in the size of the areas considered, I interpret the figures in Table I to indicate that the climatic changes had a decreasing effect southward, with no discernible (or at least a uniform) influence south of the Isthmus of Tehuantepec in Mexico. Since many of the Scarabaeidae have poor dispersal abilities (Howden 1966), I believe that the group is a good indicator of terrestrial environmental changes. Other groups with better dispersal such as some Hymenoptera do not show similar patterns, for example, see Evans (1966). However the preponderance of evidence indicates that the most profound climatic effects on the fauna occurred in the United States and Canada. The general picture of more species occurring in southern areas has been referred to as latitudinal divergence, and discussed

in detail by Fischer (1960), Simpson (1964), and Hagmeier & Stults (1964).

The sequence of events, as indicated by the present-day biota, was first a division of the forest habitats by mountains, prairies, and deserts into eastern and western formations. These in turn were further fragmented by glaciers in the north and by wet and dry cycles to the south. The climatic cycles resulted in repeated advances and retreats of mountain forests in the west and southwest and of expansion and contraction of coastal waters, particularly in the east, resulting from changes in sea level (Olson et al. 1954; Howden 1963). These changes, and the resulting isolation and fusion, undoubtedly influenced the composition of the biota, particularly on the species level. A series of papers published in a volume on "The Quaternary of the United States" (Ross 1965; Frey 1965) gives a number of examples of this effect.

The difficulties encountered in attempting to decide what happened to a certain group of insects at various times during the Pleistocene have seemingly discouraged speculation on the precise effect of any glacial maximum except the last. Papers dealing with the development of the insect fauna in North America seem to make more definitive statements about pre-Pleistocene times than they do about those of the Quaternary. There are few exceptions to this, even in non-entomological literature. Mengel (1964) has speculated on the effects of the Pleistocene on the formation of species in some northern wood warblers (Parulidae). He presents a very interesting analysis of the development of the group, starting with pre-Pleistocene conditions. The geographic separations of populations by glacial intrusions are mapped for each of the four major glacial and interglacial periods and the effects of the separation of populations is correlated with the speciation of the warblers. A similar study has been done by Smith (1966) in his work on the "Evolution of some arctic gulls (*Larus*)."

There have been parallels to this type of paper done on a few groups of insects but none that cover either the entire Pleistocene or a group that essentially occurs throughout most of North America. I have speculated on the general effects of the various climatic changes of the Pleistocene on certain genera of scarabaeid beetles (Howden 1966), mentioning that speciation in such genera as *Serica* in the mountains of the southwestern United States must have been influenced by the alternating wet-dry cycles that have occurred. These cycles were responsible for the fusion and fragmentation of the montane forests (Martin 1958), and since *Serica* is largely limited to oak (*Quercus*) forests, the fusion and isolation of populations almost certainly has strongly influenced speciation as we now see it. However, no attempt was made to correlate the time of speciation of our present species groups with any particular glaciation.

Seemingly, some of the most important evidence that has so far emerged from entomological studies on the effects of the Pleistocene deals with the mobility of many insect populations. Many earlier papers, particularly those dealing with vertebrates, have left the impression that there was

extensive migration in front of the advancing ice. This undoubtedly is true in some groups with a high mobility. However, there has been too little thought among biologists as to the rapidity of ice movement. In discussions with Dr. V. K. Prest and other Pleistocene geologists of the Geological Survey of Canada, I was informed that ice build-up and movement, at least during the last maximum, was so rapid that many sedentary organisms, including many smaller plants, may not have had the ability to survive by migration. The original snow accumulation must have occurred over a larger area. Once the cover was sufficient to form ice thick enough for lateral movement, the movement was not uniform. Periods of stability alternated with advances or surges of ten or more feet per day. Total movement may not have been more than 175 or 200 feet per year, but during the time of a surge many sedentary organisms were probably eliminated. This extinction has, in a general way, already been discussed in the explanation of Table I. In considering relatively sedentary insects at the species level, there is considerable evidence that the survival of many species occurred just south of the ice and that their survival was due to their occurrence in this area prior to the glacial advance. Alexander & Moore (1962) have demonstrated this very well in their analysis of the 13-year and 17-year cicadas (*Magicalcada*). In a series of maps they have shown that a number of the broods survived only slightly to the south of the maximum Wisconsin glaciation and have reinvaded, only to a slight degree, glaciated habitats. Hubbell (1960), in his work on bird-locusts of the genus *Schistocerca*, postulates for the species *lineata*,

. . . that, in spite of Pleistocene expansions and contractions, the range of ancestral *lineata* had for its core the central and southern Prairie-Plains, where the modern form of the species finds its optimum environment and occurs in greatest numbers, most varied forms and with least restriction of habitat. Current uncertainties as to the distance to which the ice sheets exerted an influence on the climate, and debate concerning the amount of southward shift that took place in the biota during the glacial maximum (Deevey 1949; Martin 1958) scarcely affect this particular point, since the climatic changes recorded by the fossil vertebrate faunas in the late Pleistocene deposits of Meade County, Kansas (Hibbard & Taylor 1960) do not seem to exceed the differences tolerated by *lineata* over the extent of its modern range."

In scarabaeid beetles, nearly every species occurring today in the areas covered by the classical (last) Wisconsin glaciation have some portion of their present range occurring outside of the glaciated areas (Howden 1966). Lindroth (1965) has studied the flora and fauna occurring beside a present-day glacier in Iceland, and his lists of plants and insects surviving in the immediate proximity to the ice are impressive. The conclusion to be drawn from the evidence presently available is that, in relatively sedentary groups, there was no large migration southward in front of the ice, but rather, survival of that portion of the population that was able to survive *in situ* in a habitat already occupied before glaciation.

The above is perhaps an oversimplification, since, as ice built up in the



North, the sea level was lowered by as much as 400 feet, exposing large areas of the continental shelves (see map). These newly exposed areas represented a considerable, previously unoccupied, land area particularly along the eastern seaboard, which then became available for occupancy. Coastal species probably moved seaward with a resulting shift of other populations. The magnitude of this shift for most insects was probably one or two hundred miles and, while it possibly explains the survival of many southeastern species, it did not constitute an area freely available to many northern species, with the possible exception of exposed areas in the vicinity of Newfoundland, Nova Scotia, and coastal Alaska.

#### EFFECTS IN EASTERN NORTH AMERICA

The various portions of North America east of the Great Plains, are best dealt with by region. Studies of the southern portion, particularly Florida, have played a major role in the attempts to answer the questions concerning sea level change and the degree of climatic change, questions that have long been subjects of debate. The unique characteristics of a considerable percentage of the Floridian biota have been known for many years and have caused considerable speculation concerning the area in which the Quaternary biota survived. Hubbell (in Olson et al., 1954) was one of the first to postulate (despite the adverse geological evidence of that time) that it was unlikely that all of central peninsular Florida had ever been entirely inundated by the Pleistocene seas. In his discussion of the beetle genus *Mycotrupes* he suggested that the evolution of the genus indicated an *in situ* development, with the isolation of species dependent on the formation and fusion of islands formed by changes of sea level. Since Hubbell's work, other evidence, both geological and biological, has strengthened his hypothesis. Other beetles in the families Meloidae (Selander 1960) and Scarabaeidae (Howden 1963, 1966), lycosid spiders (McCrone 1963), the orthopteran genus *Melanoplus* (Hubbell 1956), some Mollusca (Clench & Turner 1956) and a variety of other organisms have been shown almost certainly to have survived the Pleistocene changes in some part of peninsular Florida. Graham (1965) reviewed the botanical evidence, particularly that stemming from pollen analysis, and concluded that, "it is more likely that although the ranges of certain species [of plants] were modified during the Pleistocene, the general effect of climatic changes on the biota of southeastern United States was not extensive." "Extensive" perhaps is not the best word, since the pre-Pleistocene "biota" possibly was richer than that of today; nevertheless, many genera and species survived in the Floridian area.

If the evidence of a Pleistocene Floridian refugium is accepted, there still remains the question of climatic influence. Dillon (1956) argued, correctly, I believe, against the theory of a uniform, world-wide depression of temperature during glacial maxima. Temperatures undoubtedly were depressed in the southeastern United States and Frey (1965) summarizes the very strong evidence for this presented by marine biologists. Some flightless genera of scarabacid beetles occurring in the sand hill regions of Florida at

present have unusual winter time activity patterns, and by a comparison with related groups, I inferred (1963) that the summer climate of central Florida during the Wisconsin glaciation was possibly equivalent to the summer climate (July mean of 65.3° F) of Marquette, Michigan, today. Winter climate due to the maritime influence, was still fairly mild, with a January mean of perhaps 35° F (Dillon 1956). The reasoning and accuracy of this leaves a wide margin of error, but a careful analysis of temperature tolerances in different groups of insects could prove useful when combined with speculations on past distributions.

North of Florida the exposure of large coastal areas (see map) during periods of maximum glaciation allowed the survival of much of the fauna well to the north. Recent discoveries (Whitmore et al. 1967) indicate that mastodons and mammoths ranged widely along coastal areas now submerged, and Munroe (1956), suggested that certain insects now endemic to the Gulf of the St. Lawrence probably survived the glaciations on or near the Grand Banks off the coast of Newfoundland.

Many eastern species of insects apparently survived just south of the ice. The work of Alexander & Moore (1962) on the *Magacicada* has already been mentioned. Reichle (1966) has shown that many species of pselaphid beetles are now found in bogs along a line that approximates the southern limits of the last glaciation. He suggests that their dispersal powers are limited and infers that they survived immediately to the south of the glacial limits. The survival of populations south of the ice was fragmentary, species being divided into "pockets" to the east or west of the Appalachian Mountains or in the Ozark mountain region. Isolation of populations in some cases did not result in further speciation, although in some cases east-west populational differences in one species can be distinguished, as is the case in *Lytta sayi* (Selander 1960). In winter stoneflies of the genus *Allocahnia*, Ross (1965) postulates a separation during the last glaciation of populations on either side of the Mississippi River, which resulted in the formation of two sister species, *A. recta* and *A. mohri*. A similar case occurs in the scarabaeid genus *Osmoderma* (Howden 1968), where two species now occur largely to the east of the Mississippi River and one to the west. The east-west pairing of species is a common phenomenon, both within the forested areas of eastern North America and in east and west coast forest forms, with the latter having occurred, in general, in early Pleistocene or before.

In the glaciated area of the east, and here I refer mainly to the New England, Quebec, Ontario, and the Canadian Maritime provinces, glacial recession occurred more recently than in the west (see map), with areas in northern Quebec being ice-free for less than 7000 years. The recession, once started, was fairly rapid, averaging perhaps 400 to 500 feet per year (Davis 1961). Reinvasion by forests according to Davis (1961), was slower, even under good conditions, since the rate of glacial retreat was approximately twice as fast as post-glacial spruce migration as measured in Swe-

den. The mobility of the flora (Davis 1965) is very important to plant-associated insects since, even if the insects are highly mobile, their establishment depends on the presence of their host. Because of the interaction of factors, little has been done with the rate of reinvasion by insects of the glaciated areas, but fortunately the reinvasion patterns can be deduced in some cases. A good example of this is the paper on "Postglacial colonization of Canada by its subboreal winter stoneflies of the genus *Allocaonia*" by Ross and colleagues (1967) in which it is shown that reinvasion is not necessarily a general northward movement, and that climate in itself may not be the major factor in limiting northern dispersal. W. J. Brown (in an unpublished MS) has concluded that the beetle fauna of northern Quebec and Labrador originated largely from unglaciated areas to the south with the Hudson Strait being an effective barrier, since twice as many species occur on the southern side of the Hudson Strait as on the northern side.

#### EFFECTS IN CENTRAL AREAS OF NORTH AMERICA

The North American continent by definition includes Mexico and, to some geographers, Central America. Effects of the Quaternary south of the Isthmus of Tehuantepec are subtle and may have been largely dependent on changes of sea level. For readers interested in this area the papers by Wenzel & Tipton (1966), Hershkovitz (1966), Savage (1966), and West (1964) will furnish an introduction to the literature and problems of the area. The montane forested areas of Mexico contain a relatively old pre-Pleistocene insect fauna, many elements of which have long been separated by a continuous band of arid land from the forest faunas of the United States (Martin & Harrell 1957; Howden 1963, 1966; Cohn 1965). Papers by Cohn (1965) and West (1964) present a good summary of the historic aspects of the development of the Mexican biomes and Halffter's paper (1964) indicates the zoogeographic complexity of the insect fauna. Except for papers dealing with the insects of the northern desert areas, including Baja California, there is a dearth of information about the Pleistocene effects on Mexican insects.

The extent and permanence of the Chihuahuan and Sonoran deserts during the pluvial periods of the Pleistocene are debatable subjects. Pollen analysis shows evidence of a much wetter and cooler climate in Arizona, New Mexico, and Texas during glacial periods (Martin 1964), while the work by Wells (1966) and Wells & Berger (1967) on the flora found in fossil wood rat (*Neotoma*) nests indicate a lesser degree of change. Some of the best evidence of the permanency of the deserts, both as a barrier to faunal exchange and as an area for survival, is entomological. Cohn (1965) gives a detailed reconstruction of the history of the arid-land orthopteran genus *Neobarrettia*, relating the evolution of the genus to the geological and climatic changes of the Tertiary and Quaternary. Van Dyke (1939) discussed the large, desert-adapted beetle fauna and concluded that it had, because of its size and diversity, a long evolutionary history in essentially the

same area as is occupied today. Specifically, the arid-land or desert formations were certainly reduced in size (Howden 1963, 1966) but were not reduced to the extent that the insect fauna was largely eliminated.

The effects of the Pleistocene climatic changes on the Great Plains fauna has been difficult to detect, but almost certainly has been largely a north-south shifting that was dependent on climate (Hubbell 1960; Ross 1965). The plains area, throughout the Pleistocene, continued to be, to a great extent, a barrier to east-west dispersal of forest faunas. The Black Hills of South Dakota today show an odd mixture of eastern and western forest insects, but this mixture may be recent and, as suggested by Ross (1965), the invasion of the area could have been along "narrow gallery forests along stream banks." There is little or no evidence of insect species being endemic to the Black Hills region.

#### WESTERN NORTH AMERICA

The Pleistocene effects on the fauna inhabiting the extremely varied and complex western topography are difficult to interpret. The insect fauna of both Baja California and California is an old one (Howden 1963), surviving the glacial periods largely *in situ*, and the degree of the speciation attributable to the Pleistocene is largely speculative. Truxal (1960) discusses the affinities of the entomofauna of Baja California and noted the Sonoran affinities. The faunas of Sonora and Baja California, while having some affinities (Evans 1966; Howden 1963) differ in many ways, with Sonora the more important center for post-glacial dispersal of arid-adapted insects. The survival of semidesert-adapted insects during glacial periods was not limited to the Californian, Sonoran, and Chihuahuan regions. The Great Basin region of Utah and Idaho has a number of endemic species of insects (Linsley 1963) and since they occur only in the Great Basin region today, the endemic fauna (although a small one) has probably survived in this area throughout the Pleistocene. The same *in situ* type of survival is probably true in the case of the coastal and foothill fauna, as seems to be the case in the genus *Pleocoma* (Howden 1963). Ross (1965) states that some caddisflies occurring "especially in Oregon and California, appear to have moved northward very little and might indicate that few temperature changes occurred in some of the lowland Pleistocene climates of that area." At higher elevations, montane glaciation separated populations of some groups. Ball (1966a) speculated that some ground beetles in the genus *Scaphinotus* having boreal affinities were able, during cooler periods, to invade and speciate in the southwestern mountains of Arizona during the times of forest expansion and contraction.

Using Lepidoptera as an example, Munroe (1963) stated that, "In the Southwest there were extensive pluvial stages, perhaps corresponding to the glacial stages in the North. These probably permitted mixing of the faunas now isolated in the Mountains of southern Arizona and New Mexico, explaining their relative lack of diversity." Differences in dispersal abilities be-

tween Coleoptera and Lepidoptera (Schneider 1962) almost certainly explain these different interpretations of the effects of past events expressed by Ball (1966a) and Munroe (1963). Before any definite conclusions can be reached concerning the western entomofauna, careful analysis of many groups of western insects is needed.

Between the southern edge of the ice along the British Columbia-United States border and the unglaciated areas of Alaska and the Yukon (see map) there is probably no area in which any appreciable number of insects survived during the Wisconsin. During the last glacial recession, insects invaded newly exposed areas both from the south and from the Alaskan area. Since the fauna of the latter area is distinct in many ways from the unglaciated areas to the south, it is treated separately.

#### THE BERINGIAN AREA AND NORTHERN REFUGIA

The Beringian area, composed of Alaska and the adjacent areas of Siberia, was largely unglaciated (Colinvaux 1967) at least during the Wisconsin. During this time, lowered sea levels exposed large areas of the continental shelf, forming a continuous land bridge between Alaska and Siberia (Carlquist 1965). Many species of insects were able to survive in the arctic tundra environment and during interglacial periods spread to the east and south. Present-day similarities of the fauna between Siberia and Alaska are striking. Holland (1963) has shown that 50 per cent of the fleas occur in both areas, with some differentiated at the subspecies level. The fleas fall into two major distributional patterns, one being amphiberian with post-glacial dispersals east and south, the other Nearctic, resulting from southern invasions. In the ground beetle subgenus *Cryobius*, Ball (1966b) suggests a long developmental history, not only in the Beringian area but in the unglaciated "Mackenzie District Refugium" near the mouth of the Mackenzie River. Ross (1967) has evidence that the caddisfly (Trichoptera) fauna has crossed the Bering bridge a number of times during Pliocene-Pleistocene times and perhaps in recent times, a similar picture is given for the orthopteran genus *Chorthippus* by Vickery (1967). Ross (1964) believes the same is true of some mosquitoes, particularly *Aedes cinereus*. Lindroth (1963) considers the Aleutian Islands as a secondary route of migration, distinct from the Bering Strait area, basing his arguments on evidence derived from plants and insects (Carabidae).

The evidence in support of an unglaciated "refugium" in Alaska is strong, but our knowledge of the origins and dispersal patterns of arctic insects is still meager, partly because of special problems centering on the severity of the environmental conditions. Mason (1958) discussed some of these problems as encountered in Alaska, indicating that the Beringian and Nearctic elements probably need further subdivisions. Downes (1964) has discussed the "Arctic insects and their environment," covering not only the environment and its influences but the origin and affinities of the fauna. In two papers, McAlpine (1965a, 1965b) describes the insect fauna (particu-

larly Diptera) found on northern Ellesmere Island and on Ellef Ringnes Island. In the discussion of Ellef Ringnes he considers dispersal problems and the recent origin of the fauna, which may be from the East rather than from the West.

Part of the uncertainty as to the origins of various insect species revolves around the problem of arctic refugia, other than Alaska. Downes (1966) has shown that the northern Greenland lepidopterous fauna is the same as that of high arctic Canada. In contrast, he believes that the lepidopterous fauna of southern Greenland is largely adventitious and of post-glacial age. W. J. Brown (unpublished MS) has analyzed the beetle fauna of the eastern Canadian arctic, the post-glacial invasion of most species being either from Alaska (west to east) or from southern areas. As mentioned earlier, the Hudson Strait, as well as Hudson Bay, seemed to serve as barriers, as some of the Baffin Island beetle fauna is western rather than southern in origin according to Brown. A very small percentage of species seem to be endemic to the high, eastern arctic area. In order to explain their presence a number of authors have felt that a Pleistocene refugium must have been present on either Peary Land or Ellesmere Island. Downes (1964, 1966) has discussed some aspects of the problem and states that a solution, in part, "depends on a closer taxonomic examination of the far northern populations than has yet been made."

The above statement, in reality, could be expanded to include all of our insect fauna, for only through a better understanding of the taxonomy, habits, and zoogeography of insects can we solve many of the debatable problems mentioned in this paper.

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